

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024

Number 3560, 15 pp., 3 figures, 1 table

March 8, 2007

New Genus and Species of Extinct Miocene Ringtail Possums (Marsupialia: Pseudocheiridae)

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ABSTRACT

The first unique genus of ringtail possums from the Riversleigh World Heritage Area in Australia is diagnosed and described. *Gawinga aranaea* is the type and only species of the new genus and is known from nine isolated lower molars. It has been recovered from three Riversleigh deposits: two are of early to mid-Miocene age, while the age of the other has yet to be determined. The new possum is larger than Oligo-Miocene species of *Paljara*, *Pildra*, and *Marlu*, but smaller than most extant taxa. It is characterised by a distinctive lower molar cusp morphology of parallel ridges extending primarily from the cristid obliqua, filling the occlusal basins. Additional autapomorphies include: extended, shelflike protostylid cristids and a bisected posthypocristid on m1, and posterior molars that have a metaconid ridge posterobuccal to the metaconid and an anteriorly positioned protoconid relative to the metaconid. It also possesses an enlarged protostylid on m1, a feature otherwise known only in extant genera. The precise phylogenetic position of *Gawinga* within the pseudocheirid radiation has yet to be determined, but it is tentatively identified here to be a highly derived pseudocheirid, apomorphic with respect to *Paljara* and *Pildra* species, and with no known descendants.

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INTRODUCTION

The ringtail possums and greater glider family (Pseudocheiridae) comprise a group of reclusive, nocturnal, arboreal marsupial folivores. They form one of the most diverse groups within the broad radiation of diprotodontians (possums, kangaroos, koalas, and wombats). The breadth of diversity within the group was formally recognized in 1987 with its elevation from subfamilial to familial status (Aplin and Archer, 1987). This followed increasing evidence from molecular studies that pseudocheirids form a much more distinct lineage than previously thought (e.g., Kirsch, 1977; Archer, 1984; Baverstock, 1984).

Extant pseudocheirids belong to six genera throughout Australia and the New Guinea region (Flannery, 1994; Strahan, 1995). These genera had largely been classified as subgenera of *Pseudocheirus* (e.g., Tate, 1945). Most species are limited in distribution, inhabiting high-altitude tropical rainforest in northeastern Queensland or New Guinea (Flannery, 1994; Strahan, 1995).

In addition to extinct species of living genera, fossil taxa have been referred to four extinct genera (Bassarova and Archer, 1999; Crosby et al., 2004). The oldest pseudocheirid fossils, of the extinct genera *Paljara*, *Pildra*, and *Marlu*, have been recovered from late Oligocene to early Miocene sites in the Tirari Desert and Frome Basin in northern South Australia (Woodburne et al., 1987; Bassarova and Archer, 1999). *Pseudokoala* is the fourth extinct genus, known from Plio-Pleistocene deposits in South Australia, Victoria, and southeast Queensland (Turnbull and Lundelius, 1970; Archer et al., 1997a; Crosby et al., 2004).

Paljara, *Pildra*, and *Marlu* have also been recorded from the Oligo-Miocene freshwater limestone deposits of the Riversleigh World Heritage Area in northwestern Queensland (Archer et al., 1989; Archer, 1992; Bassarova and Archer, 1999). However, the abundant pseudocheirid material from these mid-Tertiary sites at Riversleigh is largely undescribed and unpublished, with the exceptions of *Paljara nancyhawardae* and *P. maxbourkei* (Bassarova et al., 2001). Nevertheless, preliminary studies reveal a great diversity of taxa, largely unrecognized beyond Riversleigh

(Archer, 1984, 1992; Archer et al., 1989). These include new species of known Oligo-Miocene genera, the earliest representatives of extant *Pseudochirops* and the new genus and species described in this paper.

METHODS AND MATERIALS

All described fossil material belongs to the Queensland Museum palaeontology collection, prefix QMF. Lower dental terminology follows Archer (1984; see fig. 1) and homology of molars and posterior premolar follows Luckett (1993). Higher-level systematic terminology follows Aplin and Archer (1987). Riversleigh site and system nomenclature follows Archer et al. (1989, 1995, 1997b).

Measurements were made using a Wild MMS235 Digital Length Measuring Set, attached to a Wild 3MB stereomicroscope. Length (L) represents maximum longitudinal distance; anterior width (AW), and posterior width (PW) respectively represent width of the trigonid and talonid, perpendicular to the lengthwise axis. Scanning electron micrographs were taken on an FEI Quanta 200 ESEM at the Electron Microscope Unit (EMU), University of New South Wales.

SYSTEMATIC PALEONTOLOGY

SUPERORDER MARSUPIALIA ILLIGER, 1811

ORDER DIPROTODONTIA OWEN, 1866

SUBORDER PHALANGERIDA APLIN AND
ARCHER, 1987

FAMILY PSEUDOCHEIRIDAE WINGE, 1893

Gawinga, new genus

TYPE SPECIES: *Gawinga aranaea* n.sp.

DIAGNOSIS: As for the type species until additional species are known.

ETYMOLOGY: *Gawinga* is a word meaning "possum", as spoken by the late Ivy George of Riversleigh Station, northwestern Queensland. Gender is considered to be feminine.

DISTRIBUTION AND AGE: As for the type species.

Gawinga aranaea, new species

HOLOTYPE: QMF52173, isolated right m1 (figs. 2A, 3A).

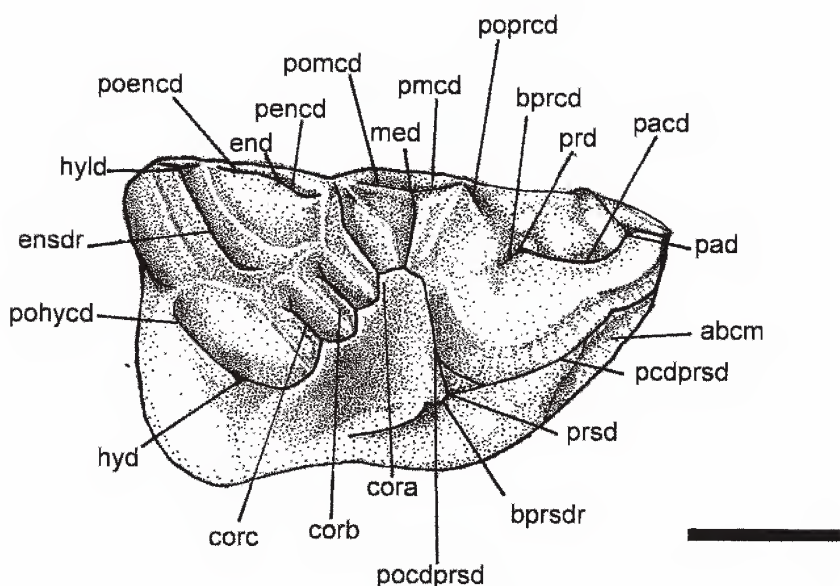


Fig. 1. Right m1 diagram of *Gawinga aranaea*. Abbreviations as follows: **abcm** anterobuccal cingulum; **bprcd** buccal protocristid; **bprsd** buccal protostylid rib; **cora** cristid obliqua ridge A; **corb** cristid obliqua ridge B; **corc** cristid obliqua ridge C; **end** entoconid; **ensdr** entostylid ridge; **hyd** hypoconid; **hyld** hypoconulid; **med** metaconid; **pacd** paracristid; **pad** paraconid; **pcdprsd** precristid of the protostylid; **pencd** preentocristid; **pmcd** premetacristid; **pocdprsd** posteristid of the protostylid; **poencd** postentocristid; **poehyd** posthypoconid; **pomcd** postmetacristid; **poprcd** postprotocristid; **prd** protoconid; **prsd** protostylid. Scale bar is 1 mm.

PARATYPE: QMF52174, isolated left m1 (fig. 3B).

TYPE LOCALITY: Arachnea Ridge Site, Riversleigh World Heritage area, Lawn Hill National Park, northwestern Queensland, Australia.

REFERRED SPECIMENS: QMF52175 (fig. 3C) right m2; QMF52176 (fig. 2D, 3I) left m4 from Arachnea Ridge Site. QMF52177 (fig. 2B, 3D) right m2; QMF52178 (fig. 3E) left m2; QMF52179 (fig. 3F) right m2; QMF52180 (fig. 2C, 3G) right m3 from Upper Site. QMF52181 (fig. 3H) right m3 from Wayne's Wok Site.

ETYMOLOGY: From the Latin *aranaea* meaning "spider" or "spider's web". In reference to the Riversleigh site, Arachnea Ridge.

DISTRIBUTION AND AGE: Riversleigh World Heritage Area, northwestern Queensland. Upper Site and Wayne's Wok Site are interpreted to be part of Riversleigh's System B strata (Archer et al., 1995, 1997b; Creaser, 1997). Biocorrelation of the Riversleigh fossil assemblages, and of Upper Site in particular, suggests an early Miocene age for System B sites. No age has been determined for

Arachnea Ridge Site, but an early Miocene age is also possible given the presence of this new species.

DIAGNOSIS: *Gawinga aranaea* is characterized by a distinct, lower molar cusp morphology as follows: a reticulated occlusal surface of robust ridges, predominantly normal and lingual to the cristid obliqua; a hypoconid base that is enlarged posterobuccally; an anteriorly placed protoconid with respect to the metaconid on posterior molars; and a bisected posthypoconid on m1. The lower molars of *G. aranaea* are narrower and longer than in most extinct pseudocheirids, with the exception of *Marlu kutjampensis* Woodburne et al., 1987, *Pildra magnus* Pledge, 1987, and all species of *Pseudokoala*. It differs from known species of the other extinct genera by having a shorter, weaker, and more posteriorly oriented m1 buccal protocristid; by having a large cusped protostylid; and a larger entostylid and ridge (entostylid completely absent in species of *Marlu* and *Pseudokoala*). Posterior molars also exhibit a prominent metaconid ridge and an elongate preentocristid that is transversely buttressed at its anterior end.

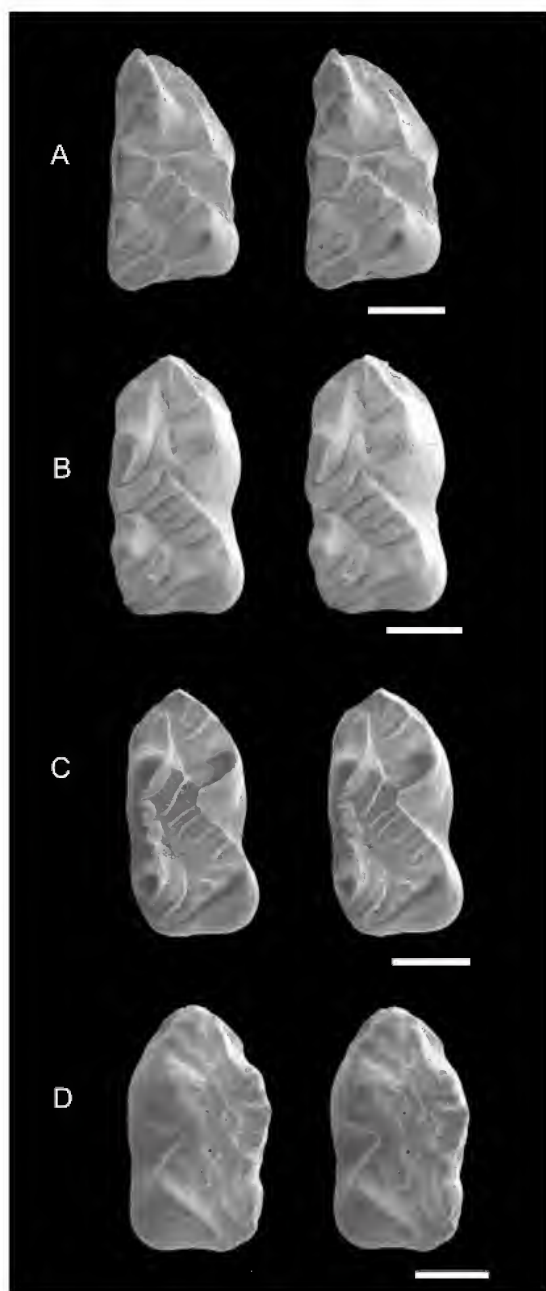


Fig. 2. Stereo occlusal view of m1–4 of *Gawinga aranaea*. A. QMF52173 (holotype), right m1; B. QMF52177, right m2; C. QMF52180, right m3; D. QMF52176, left m4. Scale bars = 1 mm.

G. aranaea differs further from *Paljara* spp. in the following features: m1 anterobuccal cingulum reduced; m1 paraconid smaller; protoconid on posterior molars buccally

enlarged; metastylid progressively more complex along tooth row; narrower notch between preentocristid and metastylid; entostylid ridge forms a continuous crest with hypoconulid; larger hypoconulid on posterior molars; more lengthwise orientation of lingual cusps, particularly entoconid; wider buccal cusp angles; buccal cusp apices less lingually curved; shallower trigonid and talonid basins. Features shared with species of *Paljara* include: m2 longer than m1; reduced or absent anterior margins between paraconid and paracristid; paraconid on posterior molars positioned on lengthwise axis; elongate, bladed metacristids; equidistant positioning of the entostylid ridge between posthypocristid and entoconid; and lack of buccal protostylid or cingulum on posterior molars.

G. aranaea differs further from *Pildra* spp. by the following features: stronger and broader anterior cingula (except *P. magnus*); anterior margins on posterior molars reduced or absent; m1 paraconid extended further anteriorly; paraconid on posterior molars positioned much closer to longitudinal axis; m1 metaconid relatively lower cusped; wider distance between apices of m1 metaconid and protoconid; narrower notch between metastylid and preentocristid; preentocristid less steep and more bladed; entoconid less conical; entostylid ridge forms a continuous crest with the hypoconulid which is separate from the postentocristid; larger hypoconulid. Features shared with species of *Pildra* include: m2 longer than m1; presence of a lingual rib extending from the m1 paraconid; lingual enlargement of the protoconid on posterior molars; progressively more complex metastylids along the tooth row; similar orientation of the posthypocristids on m1–2.

G. aranaea differs further from *Marlu* and *Pseudokoala* spp. by the following features: stronger anterobuccal cingula; larger m1 paraconid; m1 protoconid more lingually positioned; m1 metaconid relatively larger and separated from protoconid by a deeper notch; greater distance between apices of m1 metaconid and protoconid; metastylids progressively more complex along the tooth row; larger, more distinct hypoconulid. *G. aranaea* differs further from all species of *Marlu* and *Pseudokoala*, except *M. praecursor*

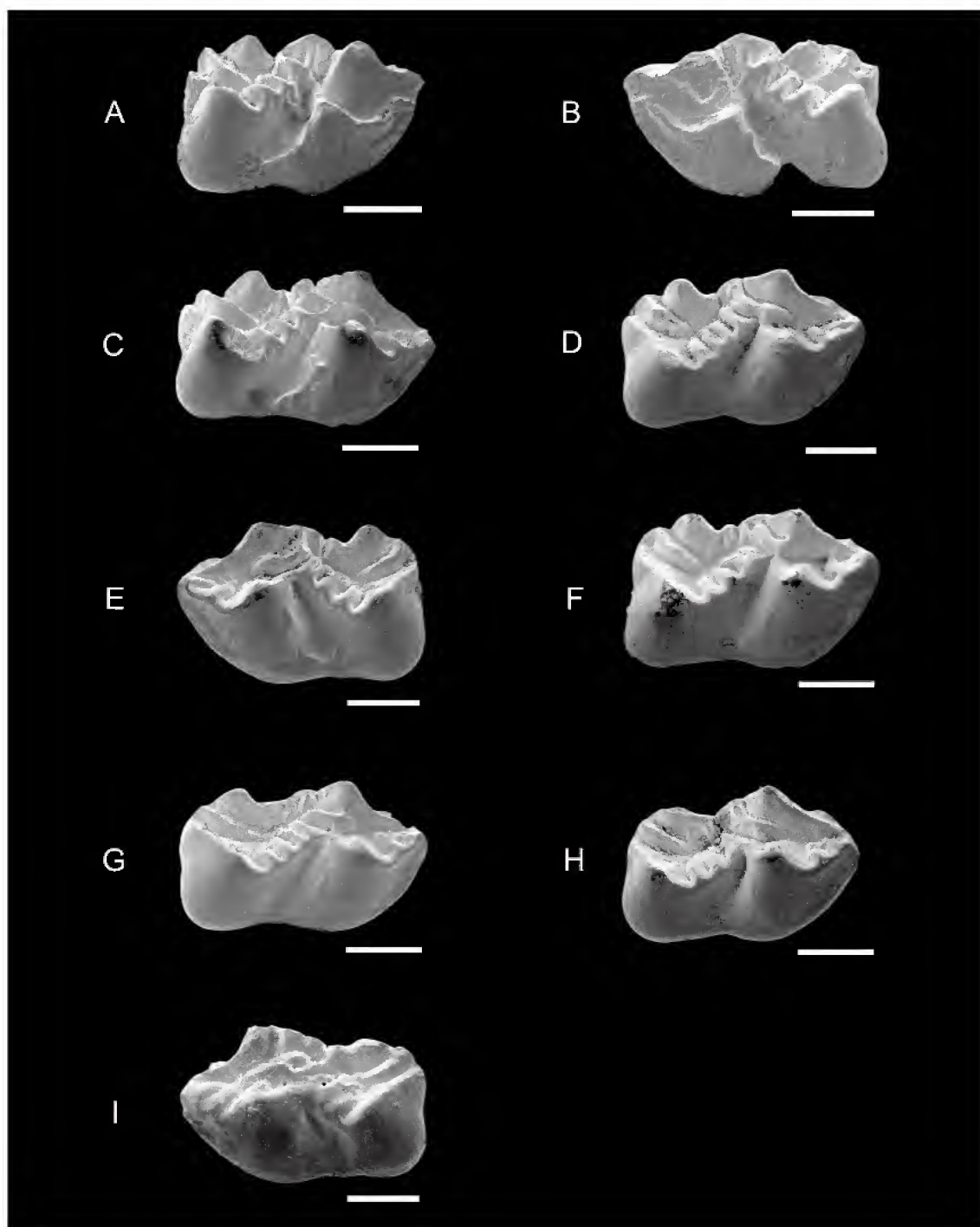


Fig. 3. Buccal views of *Gawinga aranaea*. **A.** QMF52173 (holotype), right m1; **B.** QMF52174 (paratype), right m1; **C.** QMF52175, right m2; **D.** QMF52177 right m2; **E.** QMF52178, left m2; **F.** QMF52179, right m2; **G.** QMF52180, right m3; **H.** QMF52181 right m3; **I.** QMF52176, left m4. Scale bars = 1 mm.

Woodburne et al., 1987, in the absence of an overlapping or joined metastylid and preentocristid. *G. aranaea* also differs from species of *Pseudokoala* in having relatively conical lingual cusps, with steeper cristids; shorter postprotocristid on posterior molars; posthypocristid extending further lingually and absence of a buccal protostylid or cingulum on posterior molars (except *P. curramulkensis*, originally described as *Corracheirus curramulkensis* Pledge, 1992). Features shared with *Marlu* and *Pseudokoala* species include: distinct anterolingual cingula; and broad buccal cusp angles. *G. aranaea* also shares with *Marlu* a longer m2 than m1.

In comparison with extant taxa, *G. aranaea* is smaller than all known species except *Pseudochirulus mayeri* Rothschild and Dollman, 1933, and *P. canescens* Waterhouse, 1846, and is very similar in size to *Petauroides ayamaruensis* Aplin et al., 1999. It also differs from extant taxa (species of *Pseudocheirus*, *Pseudochirulus*, *Petropseudes*, *Pseudochirops*, *Petauroides*, and *Hemibelideus*) as follows: m1 shorter than m2 (except *Petropseudes*); m1 precristid of the protostylid joins anterior end of the anterobuccal cingulum; m1 postcristid of the protostylid well-defined and shelflike, terminating at the cristid obliqua; distinct and strong metaconid ridge present on posterior molars; metastylid progressively more complex along the tooth row; metastylid and preentocristid do not overlap or join; posthypocristid more obliquely oriented.

G. aranaea differs further from species of *Pseudochirops* and *Petropseudes* as follows: stronger anterior cingula (anterior cingula absent in *Pseudochirops cupreus* Thomas, 1897, and *Petropseudes dahli* Collett, 1895); anterobuccal cingulum present on posterior molars; m1 buccal protocristid shorter and weaker; flat lingual face of metastylid; hypoconulid relatively larger and more distinct from postentocristid and posthypocristid; buccal cusp apices less lingually curved; buccal protostylid or cingulum on posterior molars absent. *G. aranaea* differs further from *Pseudochirops* spp. as follows: flat lingual face on m1 protoconid; greater distance between apices of m1 metaconid and protoconid (except *P. corinnae* Thomas, 1897); m1 pre-

metacristid not linear with very weak postprotocristid; anterior protocristid on posterior molars reduced or absent; larger entostylid and ridge, forming a continuous crest to the hypoconulid apex; entostylid ridge equidistant from entoconid and posthypocristid (except *P. archeri* Collett, 1884, and *P. winteri* Mackness and Archer, 2001); wider hypoconid cusp angle. *G. aranaea* differs further from *Petropseudes dahli* as follows: m1 metaconid much larger and separated from protoconid by a deeper notch; m1 cristid obliqua connects with metaconid; much shorter postprotocristid on posterior molars; entoconid more conical; entostylid present; less compressed lingual cristids. Features shared with *Pseudochirops* and *Petropseudes* species include: lingual rib extending from m1 paraconid and a cusped protostylid on m1. It also shares with species of *Pseudochirops* an m1 protostylid basin.

With the exception of *Pseudocheirus stirtoni* and *P. marshalli* (Turnbull and Lundelius, 1970), which are compared alongside species of *Petauroides* and *Hemibelideus*, *G. aranaea* differs further from *Pseudocheirus* spp. as follows: stronger and broader anterior cingula; anterior margins of posterior molars reduced or absent; paraconid on posterior molars positioned much closer to longitudinal axis; greater distance between apices of m1 protostylid and protoconid; m1 metaconid relatively larger and separated from protoconid by a deeper notch; premetacristid on m1 does not align linearly with the very weak postprotocristid; wider protoconid cusp angles on posterior molars; protoconid on posterior molars more lingually swollen, forming a slight anterior protocristid in some specimens; much shorter postprotocristid on posterior molars that does not unite with the metastylid; entostylid present; hypoconulid on m1–2 is not ribbed posterolingually, and is perpendicular to hypoconulid cristids; cristid obliqua terminates at same height as postprotocristid; lingual cristids on posterior molars less steep; buccal cusps less lingually curved; shallower trigonid and talonid basins. Features shared with species of *Pseudocheirus* include: lingual rib extending from m1 paraconid; a cusped protostylid on m1; and absence of a buccal protostylid or cingulum on posterior molars.

G. aranaea differs further from *Pseudochirulus* spp. as follows: anterior margins of posterior molars reduced or absent; m1 paraconid smaller and less conical; paraconid on posterior molars positioned much closer to longitudinal axis; m1 metaconid larger and separated from protoconid by a deeper notch; shorter, weaker m1 buccal protocristid; anterior protocristid on posterior molars absent or very reduced; entostylid and ridge present; hypoconulid on m1–2 is not ribbed or curved on the posterolingual surface, and cristids are oriented lengthwise; posthypocristid less curved at lingual termination; lingual cusps less conical (except m1 protoconid); buccal cusp cristids higher crested (except anterior protocristid); cristids are less steep; shallower trigonid and talonid basins. Features shared with species of *Pseudochirulus* include: broad, distinct anterior cingula and a cuspsate proto-stylid on m1.

G. aranaea differs further from *Pseudochirus stirtoni*, *P. marshalli* and *Petauroides* and *Hemibelideus* spp. as follows: anterior margins of posterior molars reduced or absent; paraconid on posterior molars positioned much closer to longitudinal axis; m1 metaconid is a more distinct, independent cuspid (except *P. marshalli* and *P. ayamaruensis*); shorter, weaker m1 postprotocristid; much shorter postprotocristid on posterior molars; entoconid buccally compressed; larger entostylid and much stronger, continuous entostylid ridge on all molars (*H. lemuroides* Collett, 1884, has no entostylid or ridge); hypoconulid more peaked and distinct and lacks a ribbed or curved posterolingual surface; wider hypoconid angles; cristid obliqua terminates at same height as postprotocristid (except *P. ayamaruensis*); buccal cusp apices less curved lingually; cristid obliqua and paracristid higher crested; buccal proto-stylid or cingulum on posterior molars absent; shallower trigonid and talonid basins. It differs further from species of *Hemibelideus* as follows: buccally enlarged m1 protostylid; m1 paraconid less conical, and independent of paracristid (*P. ayamaruensis* also differs in this feature). Features shared with *P. stirtoni*, *P. marshalli* and species of *Petauroides* and *Hemibelideus* include: distinct anterolingual cingula; an enlarged cuspsate protostylid on

TABLE 1
Length (L), Anterior Width (AW), and Posterior Width (PW) of *Gawinga aranaea*
Measurements in millimeters.

	QMF	L	AW	PW
m1	52173	3.18	1.51	1.7
	52174	3.16	1.48	1.72
m2	52177	3.51	1.82	1.81
	52178	3.29	1.78	1.84
	52179	3.23	1.57	1.63
	52175	3.38	1.77	1.73
m3	52180	3.13	1.68	1.72
	52181	3.13	1.57	1.67
m4	52176	3.31	1.73	1.69

m1; and flat lingual surfaces of metaconid/protoconid and entoconid on m1–2.

DESCRIPTION

All lower molars are relatively narrow and low cusped with shallow basins. Their occlusal surfaces appear reticulated due to the presence of enlarged ridges off the cristid obliqua and in posterior molars, also off the paracristid. Tooth homology of posterior molars was determined by differences in morphology and morphometrics (table 1).

m1: The holotype QMF52173 and paratype QMF52174 are virtually identical (figs. 3A, 3B) although the latter is slightly damaged. Lingual margin of the tooth is almost flat, and paraconid is low cusped and positioned slightly buccally to the lingual margin. A lingual rib runs halfway down the crown from the paraconid, ending in a short, horizontal shelf. Paracristid is weakly arcuate and extends down the anterior flank of the paraconid. Protoconid is subconical (missing in QMF52174), with steep, moderately bladed cristids that both curve lingually, and a steep, very weak, buccal protocristid. Protostylid is pyramidal and located midway down the protoconid; a flat, sloping lingual surface forms the protostylid basin. Protostylid cristids are long and form a shelf around the buccal protoconid face. Precristid of the protostylid descends concavely, curving back up slightly to form a small peak, a short distance before connecting with the anterior of

the anterobuccal cingulum. Posteristid of the protostylid travels posterolingually toward the metaconid, following the contour of the protoconid and hypoflexid, and terminates at the cristid obliqua. Buccal protostylid rib is kinked midway; basal half of the rib is enlarged and crested, almost reaching the base of the hypoconid. Metaconid is pyramidal with a vertical, lingual surface, defined by straight, moderately sloped cristids. Premetacristid joins the posterolingually oriented postprotocristid in a notch. The notch continues posterobuccally, forming the hypoflexid, which is traversed by the posteristid of the protostylid. Metastylid is virtually absent, comprising a very small cusp posterior to, and independent of, the postmetacristid; the triangular lingual surface of the metastylid is obliquely oriented and vertical, and its apex continues anterobuccally, merging with the anterior crest of ridge A.

Entoconid is subconical; preentocristid is anterobuccally oriented and swings transversely lingual at the end. Postentocristid is straight, running posterolingually to the lingual margin at a constant slope. Hypoconulid is also on the lingual margin and has a vertical, triangular lingual face and forms a peak directly posterior to the end of the postentocristid. Hypoconulid merges with the large, anterobuccally directed entostylid ridge, flanked by two V-shaped valleys. The ridge crest turns anteriorly following the entostylid. Posthypocristid is bisected and runs parallel to entostylid ridge; posterolingual terminus briefly deflects lingually to join posteristid of the hypoconulid, forming the posterolingual corner. Hypoconid has a flat, anterolingual surface, and is slightly shorter than the anteriorly positioned entoconid.

Viewed posterolingually, the cristid obliqua appears zigzagged. Three broad, triangular ridges run in a posterolingual direction, perpendicular to the cristid obliqua. The anteriorly directed buccal section of the cristid obliqua, before the ridges, runs from the hypoconid apex and is broadly bladed and slightly concave, like the buccal half of the posthypocristid, but shorter. Lingual section of the cristid obliqua is straight and of equal length to buccal section, and joins metaconid apex perpendicular to the metacristids.

Posterior end of protostylid posteristid joins cristid obliqua at base of this lingual section. The midsection of the cristid obliqua, connecting the buccal and lingual sections, is linear and supports three ridges, separated by equally wide notches. Ridge B is lowest in height; ridge C is broadest. Anterior end of each ridge is slightly behind the anterior end of each adjacent notch; all are joined by the cristid obliqua in a zigzag shape, so that the anterior face of each ridge is flat and leans posterolingually. Crest of ridge A curves lingually as it descends, terminating at the metastylid. Ridge C is linearly aligned with the entostylid ridge. Talonid basin is reduced to a narrow, obliquely oriented valley, parallel to the cristid obliqua.

m2: Paraconid and anterior point of tooth is extended on the lengthwise axis so the trigonid is pointed. Paraconid is distinct (damaged in QMF52175). Paracristid supports one or two posterolingual, triangular ridges, similar to the cristid obliqua ridges. In QMF52178 and QMF52177 (reduced in QMF52179) a small ridge extends posteriorly from the paraconid. A buccal rib descends from the premetacristid in all except QMF52177, typically joining a paracristid ridge. An anterobuccal cingulum descends low on the buccal enamel, either proceeding from the paraconid or a short distance below; a buccal parastylid is present, except on QMF52178. A slightly shorter anterolingual cingulum, sometimes featuring a lingual parastylid, extends horizontally from the lingual side of the paraconid, often in conjunction with anterior end of the premetacristid. Protoconid is shorter and positioned anterior to metaconid; it is a conical, lingually enlarged cusp, taller than the hypoconid. A small, short posterobuccal shelf is positioned midway down the cusp (on QMF52175), and a thin posterobuccal rib runs to the protoconid base (QMF52175 and QMF52178), possibly as a vestigial protostylid. Lingual surface of protoconid is enlarged, particularly in QMF52179 and QMF52175. The poorly bladed postprotocristid weakly curves posterolingually, toward the end of the postmetacristid. Termination of the postprotocristid varies: in QMF52178 it joins the cristid obliqua in a continuous crest; in QMF52177

it buccally joins the metaconid ridge; in QMF52175 and QMF52179, cristid obliqua and metaconid ridge are joined, postprotocristid in the former is detached marginally from this junction and connected in the latter. Metaconid has elongate, bladed cristids; premetacristid slopes gradually to lingual edge of the paraconid or slightly short of it. Postmetacristid is shorter and steeper than premetacristid; it has a small lingual deflection at its end and either joins the metastylid (QMF52179, QMF52178) or is separated by a notch (QMF52175, QMF52177).

Metastylid forms a lengthwise crest (except QMF52178, which divides into two pyramidal cusps) with a small buccal rib extending from its posterior. Immediately posterobuccal to the metaconid, a triangular ridge extends anteriorly from the metastylid (not always joined). Links between the ridge and surrounding features are variable: in QMF52179, perpendicular links at anterior end of the ridge connect it to the metaconid and postprotocristid; in QMF52175, it is joined midway by a buccal link to the cristid obliqua–postprotocristid junction; in QMF52177, the ridge joins the anterior end of the metastylid and forms a perpendicular buccal link with the postprotocristid; the ridge in QMF52178 is not connected anteriorly and is bifurcated posteriorly, of which the anterior crest joins the anterometastylid while the posterior crest attenuates toward the posterometastylid.

Entoconid is subconical and taller than the posteriorly positioned hypoconid; it has moderately sloped, bladed cristids that are oriented parallel to the metacristids. Preentocristid is anterobuccally oriented but bends anterolingually at the base, where it either levels or rises slightly before terminating. Just after inflection, the cristid forks widely, forming a steep, flat, triangular anterior surface. The entoconid narrows progressively away from apex but widens again from the inflection point, so there is a small, transverse, pyramidal buttress anterior to the preentocristid. Opposing this preentocristid buttress is the flat, posterior face of the metastylid, separated by a narrow notch. In QMF52175 (reduced in QMF52179), a buccal rib descends from the preentocristid, swinging posteriorly at the entoconid base. Postentocristid is concave and

steeper than preentocristid, extending to the lingual margin. Entostylid ridge is similar to m1, gradually ascending anterobuccally to the entostylid before receding anteriorly, terminating buccal or slightly anterobuccal to the entoconid. Entostylid ridge in QMF52177 is damaged anteriorly. Hypoconulid and hypoconid are similar to that in m1 (hypoconid is damaged in QMF52175 and QMF52177). Posthypocristid is not bisected and is almost straight with a slight posterior curve on the lingual half. Cristid obliqua is similar to that in m1, but the three ridges are lower in height and in QMF52179 curve in toward the base of ridge B instead of running parallel. Ridge C is smaller than the entostylid ridge; ridge B splits into two ridges on QMF52178 and QMF52177; ridge A splits in all except QMF52177. Talonid valley in m2 tends to widen posteriorly. Anterior termination of the cristid obliqua is variable, but is usually either joined to or separated by a minor notch from the metaconid ridge and postprotocristid junction. QMF52178 is the only specimen in which the cristid obliqua connects solely to the postprotocristid.

m3: m3 trigonid is slightly more rounded than in m2. Anterior cingula are similar to m2, except the anterobuccal cingulum is much narrower and buccal parastylid is absent. Paracristid is smoothly curved in QMF52181 but more like m2 in QMF52180. Two paracristid ridges are present; anterior ridge is shorter and oriented anteroposteriorly, both terminate in the trigonid valley, buccally of premetacristid blade. Form of the metaconid and protoconid is similar to that in m2, as is relative height and position of cusps. Postprotocristid is poorly bladed and joins cristid obliqua in a continuous curve on the longitudinal axis. Premetacristid terminates on the lingual edge of the paraconid (QMF52181) or fails to join (QMF52180).

Metastylid is bicuspid and anterometastylid is larger. In QMF52181, the anterometastylid continues into the metaconid ridge but in QMF52180 is separated by a notch. Posterometastylid has a short buccal crest and is pyramidal. Metaconid ridge of QMF52180 is joined to the metaconid and postprotocristid by shallow, perpendicular links on either side.

Entoconid resembles that in m2 but is relatively smaller, and constriction between the entoconid and anterior preentocristid buttress is reduced. Entoconid on QMF52181 is damaged, but there is a buccal rib descending from the preentocristid, as in QMF52175 (m2). Compared to m1–2: hypoconulid is obliquely oriented so the flat lingual face forms the posterolingual corner; entostylid, entostylid ridge, posthypocristid, and hypoconid are relatively smaller; entostylid is positioned closer to hypoconulid. Cristid obliqua is oriented slightly less obliquely than m1–2; cristid obliqua ridges are reduced in height and progressively widen from ridge A to C. On m3 specimens, only ridge A bifurcates, and the divergence occurs at the start of the ridge, on the cristid obliqua.

m4: QMF52176 is here considered an m4. It has a wider and longer trigonid than talonid, and the margins are curved so the tooth appears anteriorly bulbous. Relative cusp position and heights are as in m2–3. Anterobuccal cingulum is reduced to a very short and stout parastylid-like protrusion near the enamel base, below the paracristid. Anterolingual cingulum, also short, has a lingual parastylid and runs horizontally from anterior end of premetacristid. The arcuate paracristid is disrupted by two paracristid ridges, enlarged in comparison to m2–3. Protoconid is conical with unbladed cristids; a short posterobuccal ledge occurs on the protoconid, similar to that in QMF52175 (m2). Lingual expansion of the protoconid observed in m2–3, is developed further into an unbladed, anterior protocristid, directed slightly posterolingually. Protoconid angle is very wide, more similar to m2 than m3. Postprotocristid descends gradually, joining the cristid obliqua in a continuous crest. Postmetacristid is slightly steeper than m2–3.

Metastylid is bicuspid and crested lengthwise. It features short, transversely extended blades from each apex and a lower, parallel blade running the same distance from the posterior base of each cusp. The blades are separated by small notches and the cusps, postmetacristid and preentocristid are respectively separated by deeper notches. Metaconid ridge is almost straight, extending between the posterometastylid and the posterior end of the

paracristid. The ridge is swollen centrally and a second, buccal blade extends from a right angle; this second blade runs posterolingually, parallel to the metaconid ridge, and ends opposite the preentocristid buttress.

Entoconid and hypoconid resemble that in m3. Entostylid ridge is as large as in m2, but is more curved. It ends adjacent to the lingual preentocristid rib and almost forms a complete crest around the buccal entoconid surface, as in QMF52175 (m2). Hypoconid has a steeper anterolingual surface than m1–3. Both trigonid and talonid basins are completely filled by reticulated ridges off the cristid obliqua and paracristid. Cristid obliqua ridges are more sinuous than m1–3. Ridge C is largest and rather swollen while anterior ridges become progressively thinner. No ridge is divergent, but ridge B has a slightly bifurcated crest at its posterior end.

COMMENTS: QMF52176 is a damaged specimen and is tentatively identified as m4, because it differs significantly from other specimens identified as m2 or m3 (figs. 2, 3). It is possible that QMF52176 is incorrectly assigned as m4 but will remain thus until further material is recovered.

DISCUSSION

Gawinga aranaea exhibits the following pseudocheirid synapomorphies: narrow, selonodont lower molars; a distinct entostylid and metastylid; m1 cristid obliqua connecting with the metastylid, as opposed to the protoconid or protostylid; and a lingually displaced m1 protoconid (Archer, 1984; Woodburne et al., 1987). However, the distinct ridges on the lower molars of *G. aranaea* represent an autapomorphic feature that immediately separates it from all other pseudocheirid taxa.

The form of the ridges is such that the cristid obliqua and paracristid on the posterior molars are raised and the depth of the trigonid and talonid basins reduced, particularly as the ridges themselves fill the basins. This creates relatively shortened cusp height compared to other pseudocheirid genera, but no apparent decrease in the overall relative height of crown enamel. The ridges show some resemblance to crenulations present in species of *Pildra* and *Pseudochirops*, but the phylogenetic significance of these similarities is uncertain.

Interestingly, the ridges appear morphologically similar to those found in ektopodontids (particularly *Darcus* Rich, 1986), an enigmatic family of extinct possums allied with phalangerids (Pledge, 1986; 1991). The molar morphology in ektopodontids is characterized by multiple ridges arranged in two transversely oriented lophs. The ridges often bifurcate and feature smaller, accessory ribs that anastomose and reticulate at the base of the lophs (Stirton et al., 1967; Archer, 1984; Woodburne and Clemens, 1986; Woodburne, 1987). However, the similarity of cusp detail between ektopodontids and *G. aranaea* is more likely to be the result of convergence than close ancestry, as there is little besides the enlarged ridges to unite the two groups. The unusually wide molars and transverse "lophs" of the species of *Ektopodon* are very much opposite to the characteristics of *G. aranaea* or any species of pseudocheirid. Comparison is more appropriate with species of *Darcus* (although the oldest material is Pliocene in age), due to their relatively narrow, obliquely slanted molars with reduced number of ridges (Rich, 1986), and to a lesser extent with the more plesiomorphic (ridges are weaker and reticulated) Oligocene species of *Chunia* (Woodburne and Clemens, 1986). However, the ridges exhibited by ektopodontids form a disjointed crest or loph, independent of the cristids of the main cusps, whereas *G. aranaea* has unpeaked ridges that extend away from these main cristids, such as the cristid obliqua. Without the ridges, the molar detail of *G. aranaea* is unquestionably pseudocheirid in nature (e.g., the oblique, selenodont cusps, the lingually shifted m1 protoconid and the enlarged m1 protostylid). Furthermore, the accepted phylogenetic affinities of pseudocheirids and ektopodontids is to separate superfamilies — Petauroidea (Baverstock, 1984; Baverstock et al., 1987; Westerman et al., 1990; Kirsch et al., 1997; Osborne et al., 2002) and Phalangerioidea (Archer, 1984; Woodburne and Clemens, 1986; Woodburne, 1987; Pledge, 1991), respectively—with an estimated divergence date of ~45 m.y. (Springer and Kirsch, 1991).

Besides the ridges, *G. aranaea* exhibits a number of other autapomorphies. The m1 has extended, shelflike cristids of the proto-

stylid, which are not present in any other genus. The first lower molar also has an unusually long postcristid of the protostylid, it extends across the hypoflexid, obstructing the shearing plane between the trigonid and talonid and potentially restricting transverse motion of the m1 paracone and protocone. Bisection of the posthypocristid is another unique feature of m1. *G. aranaea* exhibits the first evidence of a cusped m1 protostylid in extinct pseudocheirids, a feature that until now had been regarded as a synapomorphy of extant genera. Further autapomorphies include the metaconid ridge, a cristid located posterobuccally to the metaconid on all of the posterior molars. The form and position of this ridge is similar to the anterolingual protocristid found in species of *Pseudochirops*. However, in *G. aranaea*, there is no strong link between the protoconid and metaconid ridge besides occasional small links to the postprotocristid (there is only an incipient anterior protocristid in most specimens). The ridge is variable in its connection with adjacent features, particularly at the anterior end and in QMF52176, in which it forms an additional crest. *Paljara nancyhwardae* shows a very small stylid or cusplule at the posterobuccal base of the m2–4 metaconid, which could be homologous to the metaconid ridge of *G. aranaea*.

The anterior placement of the protoconid relative to the metaconid on posterior molars is also a unique feature of *G. aranaea*, as is the swelling of the posterobuccal base of the hypoconid. However, as the only identified material of this species is a number of isolated teeth, often lacking roots, it is difficult to determine the precise orientation within the dentary.

The many autapomorphic characteristics of the lower molars justify the erection of the genus, although referable premolars and upper molars have yet to be identified. Characteristic extra ridges should be expected in them, especially the upper molars. The morphology of the lower molar dentition, particularly the m1, is highly distinctive within pseudocheirids and provides one of the best diagnostic tools in the identification of species.

Currently, *G. aranaea* is identified as one of the most derived species of the extinct

pseudocheirids with an intriguing number of plesiomorphies shared with extinct taxa, synapomorphies with extant taxa and a suite of autapomorphies as outlined briefly below.

Woodburne et al. (1987) identified species of *Paljara* and *Pildra* as the two most plesiomorphic pseudocheirid groups. Sympleisomorphies shared with *G. aranaea* include: m1 shorter than m2 in length; absence of overlapped or joined preentocristid and metastylid; and presence of an entostylid and ridge. The first sympleisomorphy is also shared with species of *Marlu* and the last with species of *Pseudochirops*. The ancestral form of the talonid (entostylid is present; the hypoconulid and posthypocristid are independent of each other; and the posterolingual corner extends further posterior than the end of the postentocristid) is shared by *G. aranaea* and species of *Paljara*, but is also found in species of *Pseudochirops*.

Generic-level synapomorphies with other pseudocheirids include: a progressively complex metastylid along the tooth row (shared with *Pildra*); an elongated preentocristid (shared with *Marlu*, *Pseudokoala*, and extant genera); a lingual rib extending from the m1 paracristid (shared with *Pildra*, *Pseudochirops*, *Petro-pseudes*, and *Pseudocheirus*) and an enlarged m1 protostylid (shared with extant genera).

Based on these features, *G. aranaea* appears particularly apomorphic in contrast to other Oligo-Miocene pseudocheirid taxa, and the many autapomorphic features make reference to a particular group difficult. At present, it also appears unlikely that any of the modern genera were derived from species of *Gawinga*. The relationships of *Gawinga* to other pseudocheirid genera are yet to be fully assessed and will be investigated as part of a larger project on the systematics and phylogeny of Oligo-Miocene pseudocheirids, incorporating a number of new taxa in preparation (Roberts et al., in prep.).

TEMPORAL AND SPATIAL DISTRIBUTION: *Gawinga aranaea* is a relatively rare species, found to date in only three of the hundreds of local faunas in the Riversleigh World Heritage area. Two of these deposits, Upper Site and Wayne's Wok Site, are considered to be part of Riversleigh's System B deposits, which have been interpreted to be early Miocene in age, or

approximately 16–23 m.y. (Archer et al., 1989, 1995, 1997b). Upper Site in particular has produced a very diverse local fauna and has been biocorrelated with the Kutjamarpu Local Fauna of northern South Australia (Archer et al., 1989, 1995, 1997b). Although Woodburne et al. (1993) argued that the Kutjamarpu LF was late Oligocene in age, Archer et al. (1997b) argued it was early Miocene. Upper Site includes species in the three Oligo-Miocene pseudocheirid genera *Paljara*, *Pildra*, and *Marlu*, representatives of the modern genus *Pseudochirops*, an additional undescribed pseudocheirid group, and *G. aranaea*. Wayne's Wok Site has also produced taxa of the three Oligo-Miocene genera in addition to *Gawinga* and shares many taxa with Upper Site Local Fauna and other local faunas attributed to System B (Travouillon et al., ms.). Numerous other petauroid and phalangeroid taxa have been recognized from both sites (Crosby et al., 2004). Many System B localities have produced local faunas with relatively high levels of diversity and relative abundance of arboreal animals. It has been suggested by Archer et al. (1989, 1995, 1997b) that such an ecological community indicates a rainforest climate similar to that found in montane New Guinea, Borneo, or the Amazon of South America.

Arachnea Ridge Site is poorly sampled in comparison to Upper and Wayne's Wok sites. Aside from the pseudocheirid material described here, only balbarine kangaroo material has been recovered from Arachnea Ridge Site. Therefore, at the present time little can be determined with confidence about the relative age of this site other than a possible early Miocene correlation with Upper and Wayne's Wok sites.

Broad changes in faunal composition between the early to mid-Miocene and late Miocene, with a general reduction in arboreal taxa, including pseudocheirids, are well documented by the Riversleigh fossil deposits (Archer et al., 1989, 1995, 1997b; Myers et al., 2001). This is thought to correlate with changes in paleoclimate at the time, relating to the formation of the New Guinea Highlands and the onset of reduced rainfall on the Australian continent (Kemp, 1984; Archer et al., 1995; Martin, 1998). This has been suggested as the cause of a shift from a closed

forest or rainforest vegetation structure to a more open structure that would be less able to support a high number of sympatric arboreal taxa (Archer et al., 1989, 1995, 1997b; Myers et al., 2001). Five genera of pseudocheirids are now recognized in the early Miocene deposits of Riversleigh, lending further support to this interpretation.

DIET: Extant pseudocheirids are one of the most strictly folivorous possum groups in Australia and New Guinea (Flannery, 1994). The energy benefits of eating leaf matter are low, requiring the ingestion of large quantities, and therefore an efficient masticatory and digestive system (McNab, 1978; Hume et al., 1984; Foley and Cork, 1992). Strict folivory is most sustainable in mammals of 700 g mass or higher, but there are known exceptions among the rodents (Kay and Hylander, 1978; Foley and Cork, 1992). All living ringtail taxa are primarily leaf eaters, but they are also known to eat fruits, flowers, and, in the smallest species, moss and lichens (Archer, 1984; Flannery, 1994). Based on molar morphology, *G. aranaea* is also considered to have been primarily folivorous. Australian pseudocheirids range in weight from just under 700–2000 g but average around 1000 g (Strahan, 1995). A body-mass estimate of *G. aranaea* from the diprotodontian m3 occlusal area prediction equation of Myers (2001) predicts a mass of 323 g. The two smallest extant pseudocheirids are the New Guinean species *Pseudochirulus mayeri* (~150 g) and *P. canescens* (~350 g) (Flannery, 1994), and like them, *G. aranaea* may have supplemented its diet with a range of food types in addition to leaf matter.

The additional ridges on the cristid obliqua and other blades are likely to have served as extra shearing surfaces. *G. aranaea* also has narrower molars than other extinct pseudocheirids, more like those of most living ringtails. These teeth are also more elongate than those possessed by primarily insectivorous, gumivorous, or omnivorous possum groups, which have stouter molars with relatively larger occlusal surfaces (Kay and Hylander, 1978).

ACKNOWLEDGMENTS

Support for the Riversleigh project has been provided by the Australian Research Council,

Queensland Parks and Wildlife Service, the University of New South Wales, the Queensland Museum, the Australian Museum and Zinnifex. We thank M. Bassarova, R. Beck, K. Black, P. Brewer, A. Gillespie, J. Louys, K. Travouillon, and V. Weisbecker for discussion, technical advice, and assistance. T. Ennis, S. Ingleby, and N. Pledge kindly allowed access to comparative specimens from the Australian Museum and South Australian Museum. We also thank an anonymous reviewer and W.D. Turnbull for valuable comments and suggestions.

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